

Growth versus storage: responses of Mediterranean oak seedlings to changes in nutrient and water availabilities

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Abstract – We compare dry mass (DM) and storage of starch (St) and nitrogen (N) in seedlings of three Mediterranean oaks, two evergreens (*Quercus coccifera* L. and *Q. ilex* L. subsp. *ballota* (Desf.) Samp) and one deciduous (*Q. faginea* Lam.), across different scenarios of nutrient and water availabilities. Three fertilization (5, 50 and 200 mg of N per plant and growing period) and watering (28–39, 55–71 and 70–85 g H₂O 100 g⁻¹ gravimetric soil water) treatments were applied to current-year seedlings between May and October 2002 in two independent experiments. The three species showed a similar response to fertilization, storing nitrogen instead of increasing biomass, in agreement with adaptations to nutrient-poor habitats. However, they differed in their responses to water, reflecting the different water requirements in the field: *Q. coccifera*, from arid zones, showed no response to water regarding DM and St; *Q. faginea*, from humid zones, required higher water availability to simultaneously increase growth and storage; while *Q. ilex*, spanning over most of the water availability range, exhibited a balanced increase of both functions when water increased moderately. In the two evergreen species, N concentration increased with water supply, whereas the reverse occurred in *Q. faginea*. The latter species favoured growth over storage at moderate water supply (according to its more competitive strategy), although it was the species which accumulated more St and N at the end of the experiments (autumn).

fertilization / N storage / seedling growth / starch storage / water stress

Résumé – Croissance par rapport au stockage : réponses de semis de chênes méditerranéens aux changements de nutrition et de disponibilité en eau. Nous avons comparé la masse sèche (DM) et le stockage d'amidon (St) et d'azote (N) chez des semis de chênes méditerranéens, deux à feuilles persistantes (*Quercus coccifera* L. et *Quercus ilex* L. subsp. *Ballota* (Desf.) Samp) et un à feuilles caduques (*Q. faginea* Lam.), pour différents scénarios de nutrition et de disponibilité en eau : trois niveaux de fertilisation (5, 50 et 200 mg d'azote par plant et période de croissance) et d'arrosage (28–39, 55–71 et 70–85 g H₂O pour 100 g de sol). Ces traitements ont été appliqués l'année en cours des semis entre mai et octobre dans deux expérimentations indépendantes. Les trois espèces ont montré une réponse similaire à la fertilisation, stockant l'azote plutôt que d'accroître la biomasse, en accord avec les adaptations aux habitats ayant une nutrition pauvre. Cependant ils diffèrent dans leurs réponses à l'alimentation hydrique, reflétant leurs besoins différents en eau dans la nature : *Quercus coccifera*, venant des zones arides ne montre pas de réponse à l'alimentation hydrique pour ce qui concerne DM et St ; *Q. faginea*, issu de zones humides, demande une disponibilité en eau plus importante pour simultanément croître et stocker, tandis que *Quercus ilex*, couvrant davantage l'étendue des possibilités de disponibilité en eau, présente un accroissement équilibré des deux fonctions lorsque l'alimentation en eau s'accroît modérément. Chez les deux espèces à feuilles persistantes, la concentration en azote s'accroît avec la fourniture d'eau, alors que l'inverse se produit chez *Q. faginea*. Cette dernière espèce favorise la croissance sur le stockage pour des apports en eau modérés (conformément à une meilleure stratégie de compétition), bien que cela soit l'espèce qui a accumulé le plus N et St à la fin des expérimentations (automne).

fertilisation / stockage d'azote / croissance des semis / stockage d'amidon / stress hydrique

1. INTRODUCTION

During the last decades extensive reforestations have been conducted by national forest services all over the Mediterranean region [41] and more recently, plantations of medium or late-succession native trees and shrubs are being promoted in spite of their poor outplanting performance [1]. Among forest species, initial seedling size or biomass has been related to post-planting survival [33], to the ability to outcompete other plant species [23] and to the potential for new root production [47], which is crucial to face the arid Mediterranean summer. In addition, carbohydrate reserves in form of starch

provide an important carbon source for both resprouting after disturbance [22] and respiration during periods of resource shortage [31]. Moreover, soluble sugars may be involved in osmotic adjustment [16] as osmolites. Therefore, carbohydrate reserves may play an important role to face the major constraints posed by continental Mediterranean climate, i.e., summer drought and winter cold [30]. On the other hand, nitrogen storage affects the rate of growth after planting in the field [25] and seedling capacity to recover foliage after disturbances [4].

Seedling biomass, carbohydrates, and nitrogen storage may vary in response to resource availability but results are still inconclusive [34, 47]. In addition, only few studies have addressed integrated response of biomass, carbohydrate and

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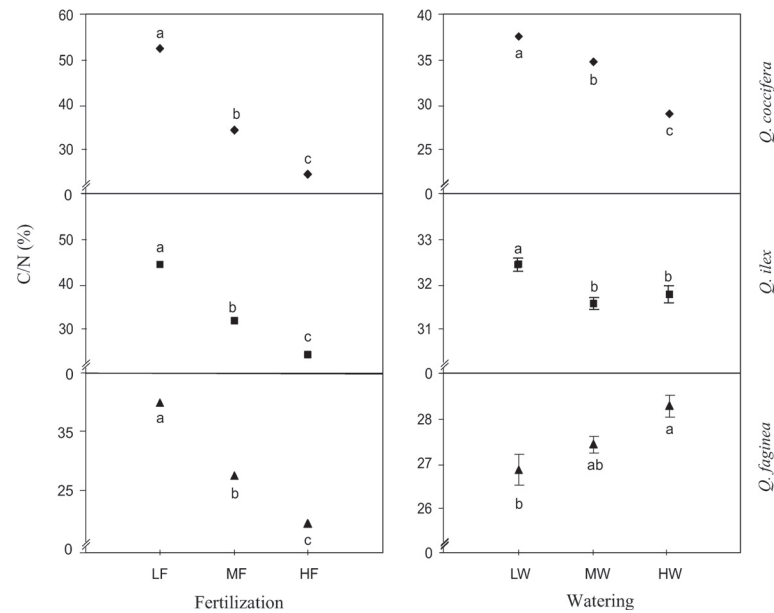


Figure 5. Effects of fertilization (left) and watering (right) on carbon-nitrogen ratio (C/N) in the whole plant. LF, MF and HF are low, moderate and high fertilization, respectively, and LW, MW and HW are low, moderate and high water treatment respectively. Values are means \pm SE ($n = 5$). Values with the same letter were not statistically different (ANOVA, Bonferroni post-hoc, $P < 0.05$).

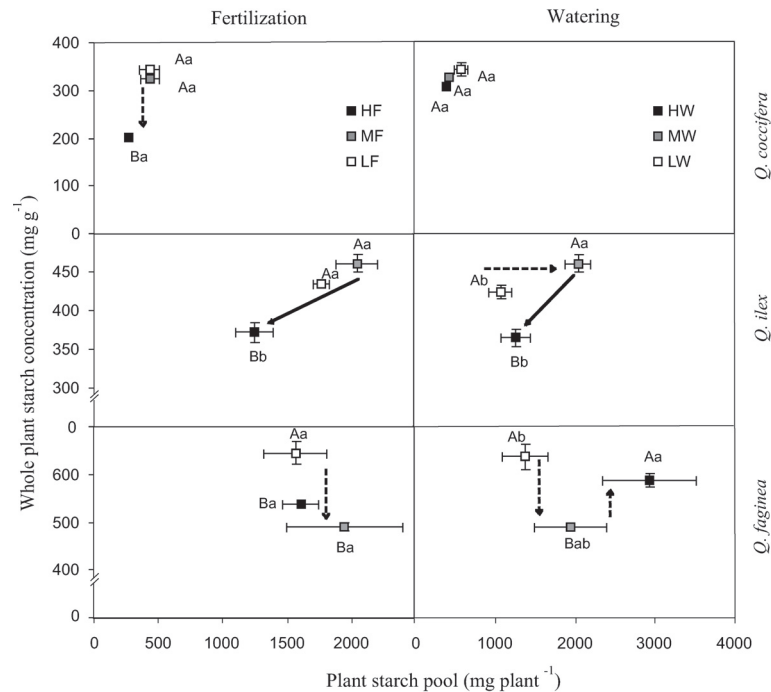


Figure 6. Effects of fertilization (left) and watering (right) on plant starch concentration (abscissas) and starch pool size (ordinates). LF, MF and HF are low, moderate and high fertilization, respectively, and LW, MW and HW are low, moderate and high water treatment, respectively. Different small and capital letters mean significant differences of starch pool and starch concentration among treatments, respectively. (ANOVA, Bonferroni post-hoc, $P < 0.05$). Arrows indicate the trajectory between two treatments which differ statistically in one (broken arrow) or the two parameters (solid arrow).

Table I. Summarised results of the two-way ANOVA testing the effect of fertilization and watering on the dry mass (DM), C/N ratio and the concentration of soluble sugars ([SS]), starch ([St]), total non structural carbohydrate ([TNC]) and nitrogen ([N]), in the whole plant and each plant fraction.

Variable	Factor	Effect of fertilisation				Effect of watering			
		Whole plant	Leaf	Stem	Root	Whole plant	Leaf	Stem	Root
Biomass	Treatment	n.s.	**	n.s.	n.s.	*	*	*	**
	Specie	***	***	***	***	***	***	***	***
	T × S	n.s.	n.s.	n.s.	n.s.	**	***	**	*
C/N	Treatment		***	**	***	***	n.s.	n.s.	n.s.
	Specie		***	**	**	***	***	***	n.s.
	T × S		n.s.	***	n.s.	***	n.s.	**	n.s.
[SS]	Treatment	***	**	***	***	***	n.s.	*	n.s.
	Specie	***	n.s.	*	n.s.	***	n.s.	**	n.s.
	T × S	***	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.
[St]	Treatment	***	n.s.	*	n.s.	**	n.s.	*	n.s.
	Specie	***	n.s.	**	***	***	n.s.	***	***
	T × S	***	n.s.	n.s.	n.s.	***	n.s.	**	n.s.
[TNC]	Treatment	***	n.s.	**	n.s.	***	n.s.	**	n.s.
	Specie	***	n.s.	***	***	***	n.s.	***	***
	T × S	***	n.s.	n.s.	n.s.	*	n.s.	**	n.s.
[N]	Treatment	***	***	***	***		n.s.	n.s.	n.s.
	Specie	***	***	***	**		***	***	n.s.
	T × S	n.s.	n.s.	n.s.	n.s.		n.s.	**	n.s.

Table II. Mean values of [SS] ± SE in the whole plant of *Q. coccifera*, *Q. ilex* and *Q. faginea* seedlings cultivated at different fertilization and watering conditions. Significance of the factors can be seen in Table I.

		Resource of availability		
		Low	Medium	High
Fertilization	<i>Q. coccifera</i>	37.55 ± 0.65	33.37 ± 0.54	14.85 ± 0.70
	<i>Q. ilex</i>	40.50 ± 0.16	23.98 ± 0.69	10.70 ± 0.59
	<i>Q. faginea</i>	50.25 ± 1.08	42.34 ± 0.40	23.26 ± 0.56
Watering	<i>Q. coccifera</i>	38.33 ± 1.34	27.70 ± 0.35	34.54 ± 0.63
	<i>Q. ilex</i>	21.41 ± 0.58	25.62 ± 0.51	23.18 ± 0.74
	<i>Q. faginea</i>	66.35 ± 0.49	34.18 ± 0.49	35.98 ± 0.98

Q. faginea (Tab. I, Fig. 7). Therefore, trajectories of N were 4–1 in *Q. coccifera* and 1 in the remaining species (Fig. 3).

3.2. Effects of watering

The response of DM to watering differed across species (Tab. I). *Q. coccifera* did not respond; in contrast the ranking of whole-plant and each fraction's DM among treatments was MW ≥ HW ≥ LW for *Q. ilex*, and HW ≥ MW ≥ LW for *Q. faginea* (Fig. 4). Although, C/N was unaffected by treatments in separate plant fractions, watering tended to decrease and to increase whole-plant C/N in the two evergreens, and in *Q. faginea*, respectively (Tab. I, Fig. 5). [SS]_{plant} exhibited

different trends with watering across species: while *Q. coccifera* and *Q. faginea* showed the highest values in LW, *Q. ilex* did the same in MW. In contrast, the three species exhibited larger [SS]_{stem} in LW in all species (data not shown). Watering had similar effects on [St] and [TNC], therefore we only described St trends. [St]_{plant} responded differently to watering across species (Tab. I): while *Q. coccifera* showed no response, *Q. ilex* exhibited similar [St]_{plant} between LW and MW that were larger than in HW. *Q. faginea* had the lowest value at MW whereas there was no difference between LW and HW (Fig. 6). St_{pool} was differently affected by watering in *Q. ilex* and *Q. faginea*, being higher at MW and at HW in the former and in the latter, respectively. Therefore, no species followed a clear St_{pool}-[St] trajectory in response to an increase of water

capacity to survive long stress periods or to recover from disturbances, which rely on stored carbon [4, 10].

4.2. Effects of watering

Irrigation induced contrasting growth and accumulation responses among the studied species. Predictions of hypothesis 2 on plant growth were only supported by *Q. faginea*, whose DM clearly increased with watering. The lack of response of *Q. coccifera*'s DM accords with the low plasticity reported for this species by other authors [7, 45], but may also be attributed to LW being not stressful enough for this species. The low tolerance of *Q. ilex* to flooding [38] may explain that this species achieved the largest DM in moderate levels of water availability.

No species supported the expected lack of watering effect on C/N, as this trait decreased and increased with watering in the evergreens and in the deciduous species, respectively. This suggests that C and N uptake increases with watering at different rates. This may be attributed to differences of stomatal conductance among species at high water supplies, which was reported to be higher in *Q. faginea* than in *Q. ilex* [28], and similar between *Q. ilex* and *Q. coccifera* [26]. Thus, the rate at which C uptake increased with increasing water supply might be more limited by stomatal conductance in the evergreens than in the deciduous species. The C/N decline promoted by watering in the two evergreens was accompanied by an increase of [N], suggesting that higher water supply induces N luxury consumption. The [St] decline shown by *Q. ilex* between MW and HW was not accompanied by significant changes of DM. Therefore, this St response may be explained by an increase of C demand for tissue respiration under the stressful conditions that higher water supplies apparently imposed to *Q. ilex* [10]. Regarding *Q. faginea*, the increased of C/N with watering was paralleled by [N] decline and by N_{pool} increase, showing that a larger proportion the plant N_{pool} was consumed by growth to the detriment of accumulation. Although [St] also declined from LW to MW, it increased again from MW to HW, suggesting that C gain at HW exceeded the amount required by growth, being accumulated for future use.

Due to their effects on DM and St, MW and HW would enhance the competitive ability [23], and would improve the capacity to keep a positive carbon balance after disturbances or stresses [22, 31], in *Q. ilex* and *Q. faginea*, respectively. However, the increase of biomass in *Q. faginea* promoted by high watering supplies was to the detriment of N storage, what would have a negative effect on the leaf recovery capacity after defoliation.

4.3. Species responses

Hypothesis 3 predicted that *Q. faginea* would give higher priority to growth than to storage at high resource supplies. Our results support this hypothesis only for N responses in the water experiment, where *Q. faginea* was the species with higher DM increase and with lower [N] increase (this trait

even declined between LF and MF) in response to watering. These responses accord with the more competitive strategy described for deciduous than for these evergreen Mediterranean trees [8, 46]. Nevertheless, *Q. faginea* was, in general, the species with largest St and N reserves. This trend was partly accounted for by the larger proportion of root biomass exhibited by this species, which was the main St and N storage organ [10, 31]. Additionally, deciduous species exhibit the greatest concentrations of St at the beginning of autumn [2], coinciding with the date of harvest in our study, while evergreens do so at the end of winter, just before bud break [14]. In the case of N, the larger leaf [N] of *Q. faginea* reflects the higher proportion of N-rich tissues in deciduous leaves as compared with evergreen ones, already reported in species comparisons in different ecosystems [8, 36]. In contrast, the evergreen species, especially *Q. coccifera*, showed higher C/N ratios, reflecting a greater proportion of structural carbon in plant tissues. This allocation pattern reflects an adaptation to stressful environments, where defensive and resistance traits may have been selected for, rather than productivity [17].

The two evergreen species allocated to leaves a greater proportion of their total N and St pools than the deciduous species, which did so in permanent organs (data not shown). This is in accordance with the storage function reported for evergreen leaves [24]. Thus, disturbances eliminating leaf biomass, would make the recovery of foliage to be slower in the evergreen species than in the deciduous one [29].

5. CONCLUSIONS

The three species showed a similar response to fertilization, storing nitrogen instead of increasing biomass, in agreement with adaptations to nutrient-poor habitats. However, high nutrient availability decreased starch reserves in all species, which may have a negative effect on their resprouting ability. Regarding watering, the two evergreen species showed the lowest C/N under high water availability while the reverse occurred in the deciduous one. The growth-storage responses to water reflected the different water requirements of the species (*Q. coccifera* from arid-zones, *Q. faginea* from humid zones and *Q. ilex* spanning over most of the range): *Q. coccifera* showed little response to water, *Q. ilex* exhibited a balanced increase of growth and storage when water increased moderately, and *Q. faginea* required higher water availability to simultaneously increase both functions. The conditions that represent the best compromise between growth and storage differ across similar and closely related species in accordance to their specific resource-use strategy.

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